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Aspects of the reproductive biology of *Polymesoda erosa* (Solander, 1786) (Bivalvia: Corbiculidae) in northern Australia

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ABSTRACT

The reproductive biology of *Polymesoda erosa* (Solander, 1786) (Bivalvia: Corbiculidae), a staple food for Aborigines in the Maningrida region of northern Australia, was studied between June 2001 and September 2002 as part of a program to manage its subsistence fishery. *Polymesoda erosa* is dioecious (gonochoristic) and matures at a shell length of approximately 45 mm. Within the range of shell lengths of 55 to 90 mm, the sex ratio in the population was 1 male:1 female. However, at shell lengths less than 55 mm, males were significantly more common. Females were more common at shell lengths greater than 80 mm, but not statistically so. At shell length greater than 90 mm, the production of new gametes is reduced. Based on the gonadosomatic index (GSI) and histological study, *P. erosa* spawned during the mid- to late-wet season (February and May). Males and females showed spawning synchrony. Females within the shell range of 65 to 85 mm produced 1.20 x 10^6 eggs per individual (SD = 0.43 x 10^6, n = 10). The high frequency of spawning was probably related to long inundation during the wet season. The present practice of not gathering *P. erosa* during the wet season may be important in sustaining the current subsistence harvest.

KEYWORDS: clams, gonadosomatic index, sex ratio, harvest, Aboriginal, mangroves.

INTRODUCTION

The mangrove clam, *Polymesoda erosa* Solander, 1786 (Bivalvia: Corbiculidae) (Fig. 1) is a large bivalve, reaching more than 120 mm in length (Morton 1985). This bivalve is naturally distributed throughout the tropical Indo-West Pacific from Sri Lanka in the west to the Solomon Islands in the east, from Japan in the north and to northern Australia and New Caledonia in the south (Morton 1984). *Polymesoda erosa* inhabits firm mud substrata surrounding streams draining through the mangroves and is capable of withstanding long periods of desiccation and wide ranging salinities. During emersion, it is able to exchange water and suspended material with subterranean water through the pedal gape, and then resume suspension feeding when inundated (Morton 1976).

Polymesoda erosa is harvested for food in various Southeast Asian countries including the Indonesian archipelago (Morton 1976, 1984). In northern Australia, *P. erosa* is a staple food of Aborigines living in coastal

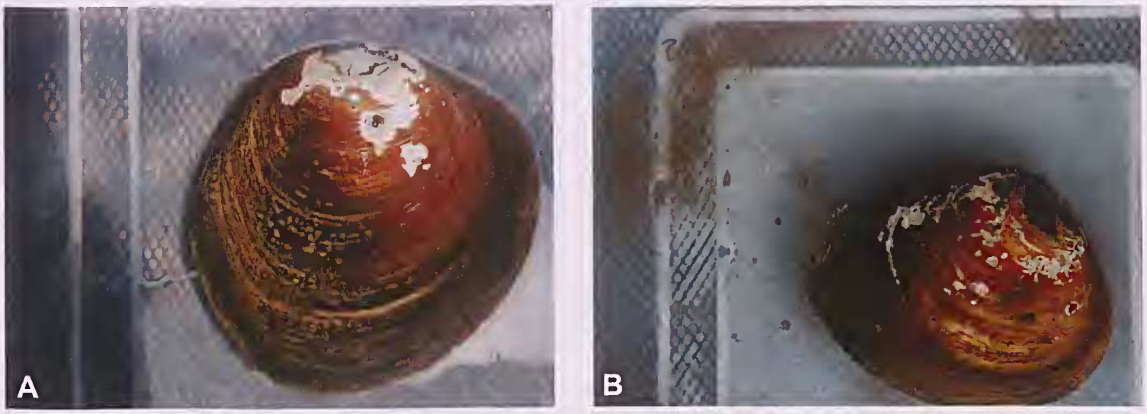

Fig. 1. *Polymesoda erosa* from Maningrida spawning: **A**, male clam ejecting sperm; **B**, female clam releasing eggs.

regions (Meehan 1982; Isaac 2002). It is the most prominent non-fish group numerically in the indigenous catch (Coleman *et al.* 2003; Willan and Dredge 2004). Despite this, *P. erosa* is not commercially harvested, although there is some potential for indigenous communities to develop commercial enterprises based on the wild harvest of species such as *P. erosa* (Ray Hall, pers. comm.). In order to do this successfully, it is important to understand, among other things, the timing of reproductive events because it is an essential prerequisite for various aspects of commercial farming and harvesting including collection of wild spat, timing of collecting season and hatchery production.

Information on the reproductive biology of *Polymesoda erosa* is scarce. To date, the study of Morton (1985) on the ecology and reproductive strategy of the species in Hong Kong is the only published work available. In Hong Kong, *P. erosa* has a single but extended spawning season during summer. Because the reproductive cycle of a species may vary considerably over its geographical range (Sastry 1979; Fournier 1992; Sato 1999; Ward and Davis 2002), a species that has a wide distribution covering several latitudes, such as *P. erosa*, is likely to exhibit a variety of reproductive strategies (Cárdenas and Aranda 2000). The present study investigated the reproductive biology of *P. erosa* from the Maningrida region of northern Australia. The results provide the basic information necessary for the farming and harvesting of this species and allows for a comparison of the reproductive strategy of the species in Hong Kong (22° 20' N, 114° 11' E) (Morton 1985) in the northern hemisphere and the Northern Territory coast (i.e. Maningrida) in the southern.

MATERIALS AND METHODS

Collections. Live *Polymesoda erosa* were collected from the mangrove forest bordering the Tomkinson River in the Maningrida region, Northern Territory, Australia (12° 3' S, 134° 13' E; Fig. 2). Temperatures and rainfalls during the study period were provided by the Bureau of Meteorology for the Maningrida region (Fig.3B, C). Salinity data (Fig. 3A) were obtained indirectly by measuring the salinity, using a calibrated hand-refractometer Vista A366ATC, of the water entrapped inside the mantle cavity when the collected individuals reached Charles Darwin

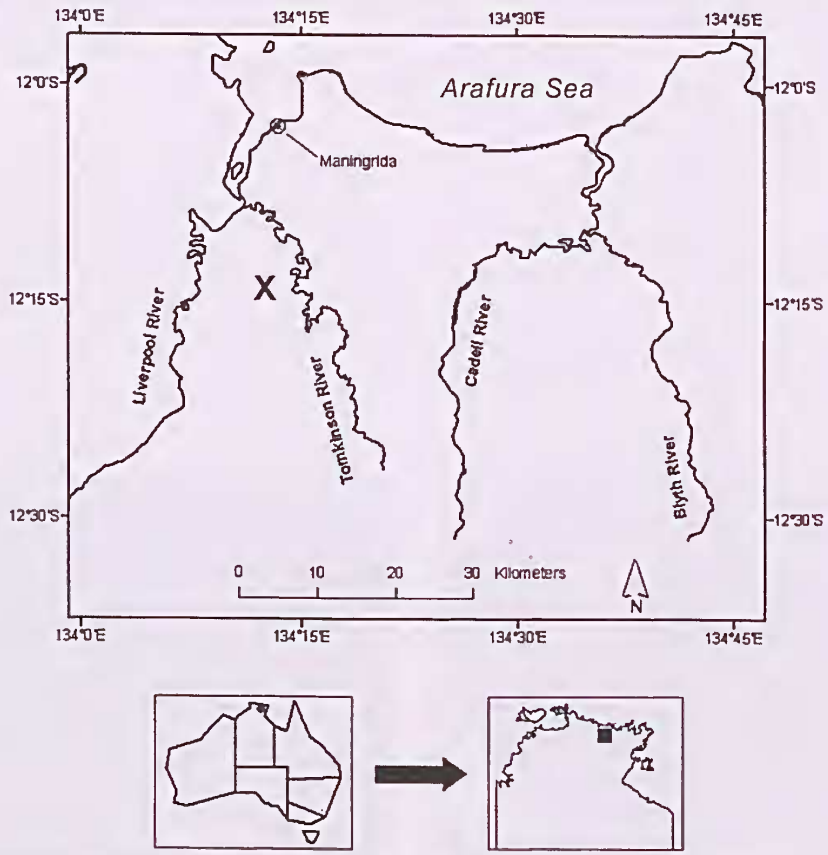

Fig. 2. Map of Maningrida region, Northern Territory, Australia, showing the collection site (x) for *Polymesoda erosa* adjacent to the Tomkinson River.

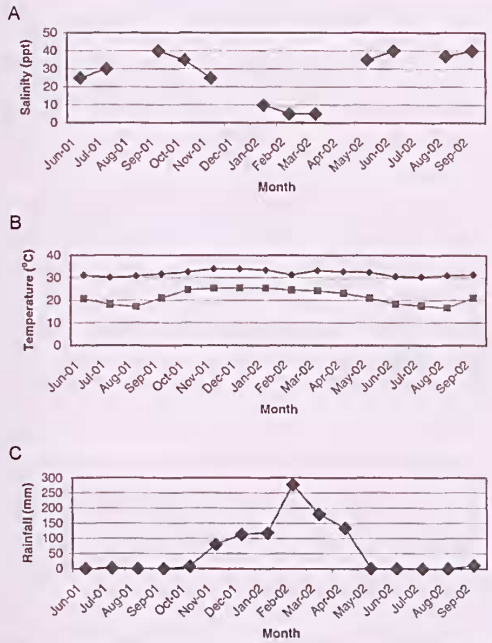

Fig. 3. A, Salinity of the water entrapped in the mantle cavity of *Polymesoda erosa* sampled at Maningrida between June 2001 and September 2002. Broken line indicates no sampling was done; **B,** Minimum and maximum air temperature recordings from June 2001 to September 2002; **C,** Total monthly rainfall (mm) recorded at Maningrida between June 2001 and September 2002.

University (see below). This was necessary because during collection the habitat of *P. erosa* was dry. From 40 to 100 individuals (31 to 112 mm in size) were taken at each sampling time spanning from June 2001 to September 2002, by digging the mud under mangrove vegetation in the hinterland margin during low tide. The animals were airfreighted dry in styrofoam boxes to an experimental hatchery at Charles Darwin University (12° 28' S, 130° 51' E). On each sampling occasion, shell length was recorded using vernier callipers.

Sex determination. The shells were opened, tissues removed and sexes recorded based on the colour of the gonad: black in females and creamy white in males. When in doubt, a gonadal smear was examined under the microscope for sperm or eggs.

Gonadosomatic index. Tissues were dissected and classified into the gonad and non-gonadal. The gonad, inclusive of stomach and intestine, was separated from other organs. Non-gonadal parts included the mantle, anterior and posterior adductor muscles, ctenidia and labial palps, pericardial organs, digestive diverticula, crystalline style and foot. Both gonadal and non-gonadal tissue were blotted dry on paper towels and weighed separately to the nearest 0.001 g with a Sartorius B310S electronic balance. Total tissue weight (TTW) was obtained by combining gonad weight (GW) and non-gonadal tissue weight (NGW). The gonadosomatic index (GSI) was calculated using the equation used by González *et al.* (2002):

$$GSI = {}^{GW}/_{TTW} \times 100$$

Histological analysis. After measurements for gonad index, the dissected gonads were fixed in aqueous Bouin's solution for 48–72 h. A central portion about 5 mm thick was dissected from each fixed gonad, placed in a tissue cassette and stored in 70% (v/v) ethanol prior to dehydration. The gonad portion was later dehydrated in FAA (40% formaldehyde, 95% ethanol, and glacial acetic acid in the ratio of 1:5:0.2) and in ascending an ethanol series ranging from 70 to 100% in a tissue processor (Shandon Duplex) overnight. The tissue was cleared with histoclear and impregnated with paraffin wax. The resulting block was sectioned at 5 mm, and sections mounted onto slides, stained with Mayer's Acid Hemalum and counterstained with eosin Y (Bancroft and Stevens 1982).

The gonadal developmental stages were assigned to criteria modified from Morton (1985) for *Polymesoda erosa* in Hong Kong (Table 1).

Gonad index. Each developmental stage was assigned a numerical score as follows: primordial = 1, developing = 2, maturing and partial spawned = 3, ripe = 4, and spent = 0. This scoring was modified from Sause *et al.* (1987) and Hadfield and Anderson (1988). For each monthly sample, a mean gonad index was determined following calculations described by Gosling (2003). The number of individuals in each stage was multiplied by the numerical ranking of the stage and the sum of these products divided by the total number of individuals in each sample.

Fecundity. Estimates of fecundity (the number of mature oocytes contained in female gonads) were made following the technique described by Dredge (1981). Mature ovaries were selected by macroscopic appearance from individuals of greater than 65 mm shell length and were fixed in Bouin's solution until hard. After washing with 70% ethanol, the membrane encasing the eggs mass was peeled off and carefully separated from the stomach and intestine. The mass of eggs was blotted dry and later weighed to the nearest 0.0001 g. A small portion from this mass was weighed and placed individually into a 250 ml beaker containing 100 ml of distilled water. A mixer was used to detach the eggs from the mass and disperse them through the water. The contents of the beaker were then transferred to a graduated cylinder and water added to a required volume. The number of eggs in the cylinder was estimated using a Sedgwick-rafter cell. The results represented the number of eggs per mass of gonad. This was multiplied by the weight of the gonad to estimate the total number of contained oocytes.

Statistical analyses. Observed sex ratios were tested against a 1:1 ratio using a chi-square goodness-of-fit (Fowler *et al.* 2000). Data for GSI from females and males were treated separately. ANCOVA with shell volume as a

Table 1. Microscopic characteristics of the reproductive stages of male and female *Polymesoda erosa* from Maningrida.

Stage	Characteristics
Males	
Primordial	Small follicles scatter gonadal area. Interfollicular space large. Phagocytes present in some follicles. Germinal cells start lining up inside of the follicle.
Developing	Dense spermatogonia in germinal layer of the follicle. Spermatozoa appear at the centre of the follicular lumen.
Maturing	Spermatozoa occupy greater area at the central lumen. The spermatozoa are in orderly stripe-configuration with tails pointing toward the centre of the lumen. Spermatocytes and spermatids are dense at the periphery of the follicle.
Ripe	Stripes of spermatozoa occupy almost the whole area of the follicle leaving a very narrow strip along the periphery for the spermatogonia and spermatids.
Partially spawned	The number of spermatozoa filling the lumen decreases in some follicles. Spermatids occupy the area vacated by the spermatozoa.
Spent	Most of follicles are empty. Empty follicles with irregular and elongated shape present in the gonadal matrix. Phagocytes are active.
Females	
Primordial	Follicles have large empty lumen. Some lytic oocytes and phagocytes present in the lumen. Few oogonia start lining follicular wall.
Developing	Follicular lumen is large. Follicles increase in size and have well defined walls. Oogonia and early-developmental-stage oocytes densely pack periphery of the follicle. Young oocytes attached to the wall by thick stalk.
Maturing	Follicles are large. Round vitellogenic-oocytes increase in size, but many still attach to follicular wall by thin stalked. Some mature oocytes with prominent nucleus and nucleolus are free in the lumen.
Ripe	Proportion of free oocytes in the lumen increase. Small number oocytes are still attached to follicular wall by thin stalk. Most oocytes are polygonal.
Partially spawned	Some follicles contain mature ova. Others are empty or contain small number of ova. Follicles reduce in size particularly in those devoid of ova.
Spent	Follicles are empty and follicular wall collapses in places. Some residual mature oocytes still present in empty lumen.

covariate was used to check for any differences in GSI over the whole year. To check whether the gonads develop in the same way in both males and females, a two-way ANCOVA with month and sex as fixed factors and shell volume as a covariate was performed (Grant and Tyler 1983). Percentage data were arcsine transformed. The frequency of individuals in the six developmental stages was tested using a contingency chi-square test (Fowler *et al.* 2000). To check to what extent the GSI can be used to follow the reproductive cycle in *Polymesoda erosa*, the GSI values were analysed using ANCOVA with the gametogenic stage as a factor and shell volume as a covariate.

RESULTS

Seven-hundred and ten *Polymesoda erosa* were collected; 361 males, 323 females, and 26 undifferentiated. No hermaphrodites were detected. The sex ratios were not significantly different from the expected 1:1 ratio for any of the 12 samples, although there were more males than females in most of them (Fig. 4). Individuals of 45–55 mm had a sex ratio significantly ($P<0.05$) biased towards males. At higher length-classes (55 to less than 80 mm) males still outnumbered females, but there was no significant ($P>0.05$) deviation from the expected 1:1 ratio. In contrast, at sizes greater than 80 mm, there was a tendency for females to predominate, although the ratio, again, did not differ significantly from 1:1.

Estimates of fecundity for ten *Polymesoda erosa* individuals within the shell length range of 65–85 mm of the above cohort showed that each clam contained 1.20 x 10^6 eggs (SD = 0.43 x 10^6).

Gonadosomatic index (GSI). The GSI of *Polymesoda erosa* varied significantly during the study period. Box and Whisker plots of gonadosomatic index for each sex showed large variability and strong asymmetry in all monthly samples (Fig. 5A, B). Each sample covered wide ranges of GSI values suggesting continuous breeding activity. However, the box plots showed differences in the positions of the medians of the data. In general, for both sexes, the medians increased from June 2001, reached a maximum in January 2002, then fell to low levels between February and May. After this period, the medians rose again and reached high values for the next three months (June to September 2002). These rises and falls in the medians were interpreted as difference in spawning intensities. The results of this exploratory data analysis were confirmed by ANCOVA which showed that the GSI values of males females differed significantly among months (males: $F_{11,107}=6.6119$, $P<0.05$; females: $F_{11,107}=6.0190$, $P<0.05$). In males, *post hoc* comparisons among means using Tukey's HSD showed significantly low values for male GSI values in February 2002 and May 2002. Similarly, in females,

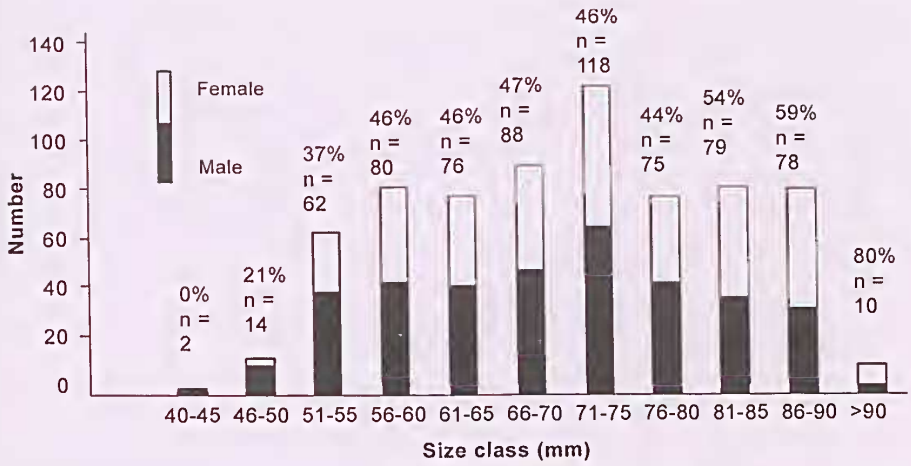

Fig. 4. Size frequency and sex ratios of *Polysoma erosa* collected from Maningrida from June 2001 to September 2002. Figures above the columns indicate percentage of female and total number of individuals collected for that size class.

significantly low GSI values occurred between February 2002 and May 2002. Two-way ANCOVA showed a not significant interaction ($F_{11,215}$=1.0773, P>0.05) between sex and sampling month, indicating that males and females have similar patterns of gonad development. However, both factors (i.e., month and sex) individually showed significant differences (month: $F_{11,215}$=11.2941, P<0.05; sex: $F_{1,215}$=84.1799, P<0.05). Females had significantly higher (P<0.05) GSI values than males. Analyses of reproductive condition by the gonad index (Fig. 6A, B) confirmed the evidence for two peaks in reproductive condition annually in both males and females, followed by troughs suggestive of spawning periods.

Male reproductive cycle. The reproductive cycle of male *Polymesoda erosa* from Maningrida is presented in Figure 7A. Contingency chi-square test showed that the frequency of each gonadal stage was associated significantly with sampling month (χ^2_{44}= 82.84, P<0.05). In June 2001, about half the individuals were in early stages (primordial and developing), while maturing and ripe were 40% and 10%, respectively. In July the frequency of the ripe individuals increased to 40% and reached a maximum between July and September. Chi-square tests confirmed that there were significantly (P<0.05) more individuals of primordial and developing stages than expected during June 2001. There was a short period of spawning during September 2001 but for the next few months until January 2002, only maturing and ripe animals were present. Seventy percent of individuals were ripe in January 2002. Starting in February, the numbers of spent or partly spawned animals increased from 20% to 50% in May 2002. During this period, the number of males with spent gonads was significantly higher than the expected values (P<0.05, chi-square test). Apparently, gonads developed rapidly after a long breeding period because in June 2002, 70% of the males were maturing and by August the sample was dominated by ripe males (50%). In September 2002, 30% of males were spent, suggesting another spawning event. The histological data for male confirm those obtained using the gonad index (Fig. 6A).

Female reproductive cycle. As in males, the frequency of each female gonadal stage was associated significantly with sampling month (χ^2_{44}= 115.98, P<0.05). The female reproductive cycle thus followed that of the males closely. All gametogenic stages occurred in most sampling months with a high proportion of maturing and ripe stages (Fig. 7B). Developing gonads, from primordial to mature, occurred during the period of June to July and, probably, through August 2001. Chi-square tests showed that these three stages had significantly higher values than expected (P<0.05) during this period. Ripe females increased during the period, and in September 50% of individuals were ripe. Some individuals spawned in September 2001 as indicated by the presence of spent and primordial stages. The ripe individuals were most common (at least 60%) during October 2001 until January 2002. An intense spawning occurred in February 2002 after which 70% of the females were spent and 10% were partially spawned. As with males, spawning activity lasted until May 2002, although intensities decreased as the number of ripe animals decreased. The mass spawning events between February and May were confirmed by chi-square tests which showed a significantly higher number (P<0.05) of spent individuals during this period. There was no resting period for the female cycle because of rapid maturation during June to August 2002. By September 2002, some of the ripe females were ready to spawn again. The histological data for females confirm those obtained using the gonad index (Fig. 6B).

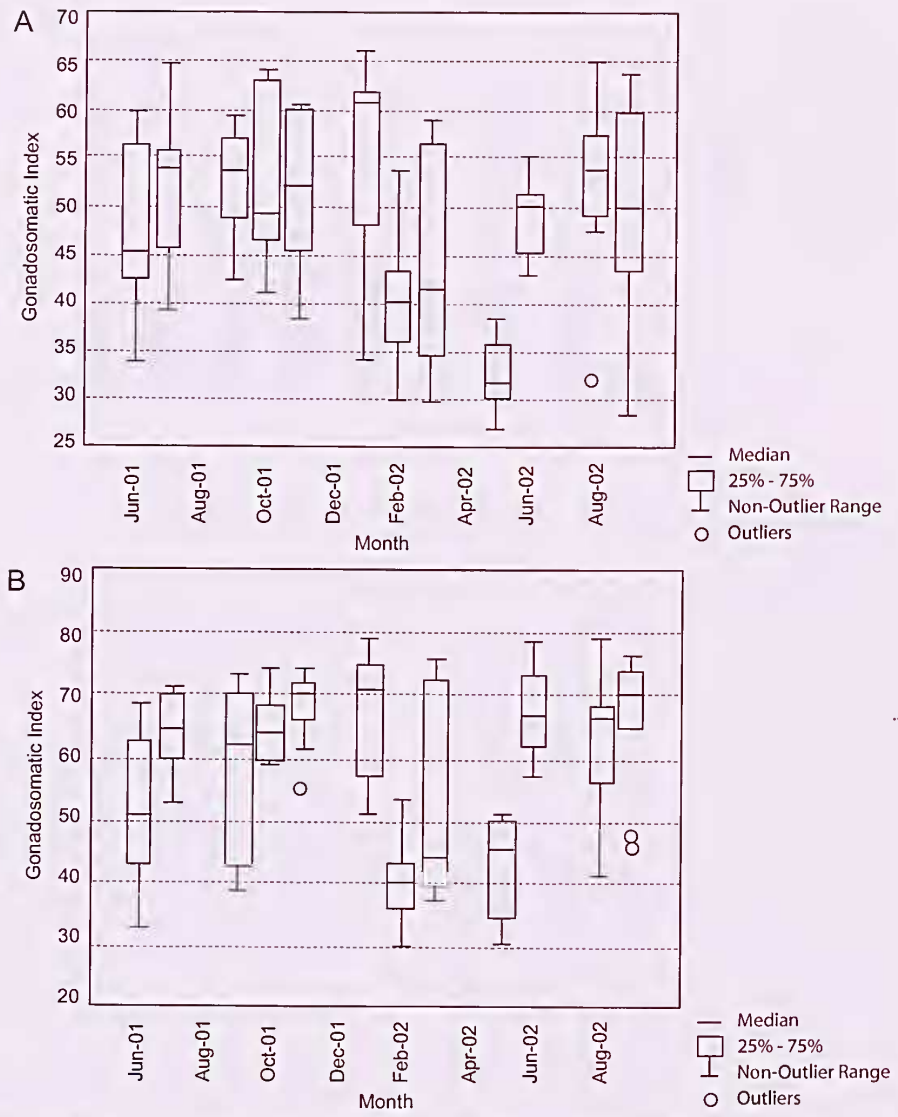

Fig. 5. Box and Whisker plots of gonadosomatic index in the monthly samples of **A,** male and **B,** female *Polymesoda erosa* individuals collected from Maningrida from June 2001 to September 2002.

DISCUSSION

Sex ratio. *Polymesoda erosa* is dioecious (gonochoristic) but shows no other morphological distinction between the sexes except for the gonads. This is in agreement with reports by Morton (1985) that *P. erosa* has separate sexes. Sexual differentiation in *P. erosa* is similar to other corbiculids, such as *P. caroliniana* (Bosc) which inhabits saline marshes (Walker and Heffernan 1994), but is different from the freshwater *P. solida* (Philippi) which is monoecious (hermaphroditic) (Rueda and Urban 1998).

Although the total number of each sex of *Polymesoda erosa* was equal, one sex predominated at certain shell lengths. Within the range of 50 to 80 mm shell length, the ratios between males and females were 1:1. However, in size classes less than 45 mm, there were significantly more males than females, whereas females were more common in the size classes greater than 85 mm. This pattern is very similar to that of the pearl oyster *Pinctada imbricata* (Röding) (O'Connor and Lawler 2004). The biased ratios in the population may be due to greater longevity in females than males, resulting in higher number of females than males in older (larger) animals, as in the case of *Arctica islandica* (Linnaeus) (Ropes *et al.* 1984; Fritz 1991; Thórarinsdóttir and Steingrimsson 2000). There is no evidence that the higher number of

females than males in the same class size is due to the faster growth rate in the former, as reported by Wells and Keesing (1989), Marsden (1999), Ward and Davis (2002) and Baghurst and Mitchell (2002). Hermaphroditism can also affect sex ratio, particularly beyond average size-classes (Littlewood and Gordon 1988; Fritz 1991; Thórarinsdóttir and Steingrimsson 2000). In the present study no simultaneous hermaphroditism was observed, which is also the case for the population of *P. erosa* in Hong Kong (Morton 1985).

Gonadosomatic index. Considerable overlaps in GSI values among months indicate that *Polymesoda erosa* has asynchronous gonad development wherein both early developed and fully mature individuals are present in the population in each sampling month. The pattern of gonad development in *P. erosa* is typical for a continuous breeder (Grant and Tyler 1983). However, although mature individuals of *P. erosa* were in evidence year round, there were differences in spawning intensities.

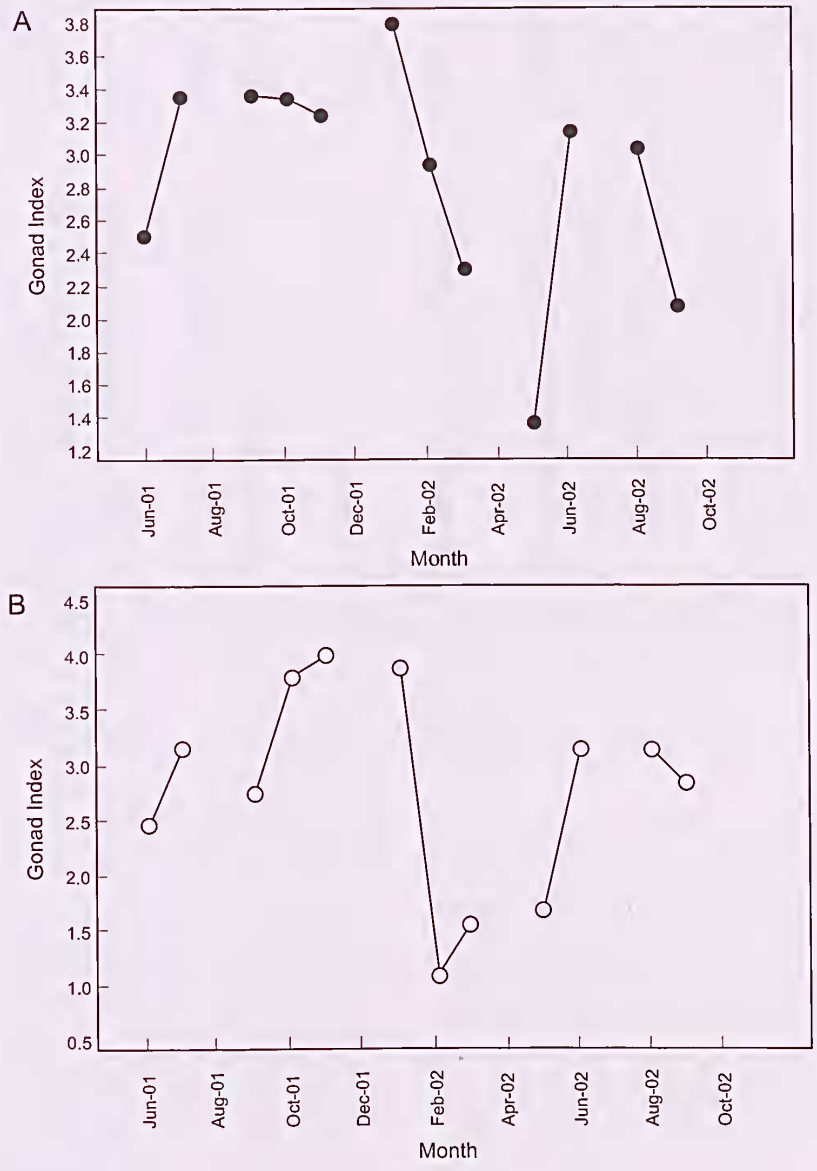

Fig. 6. Seasonal change in Gonad Index for male **A**, and female **B**, *Polymesoda erosa* from Maningrida over the period between June 2001 and September 2002.

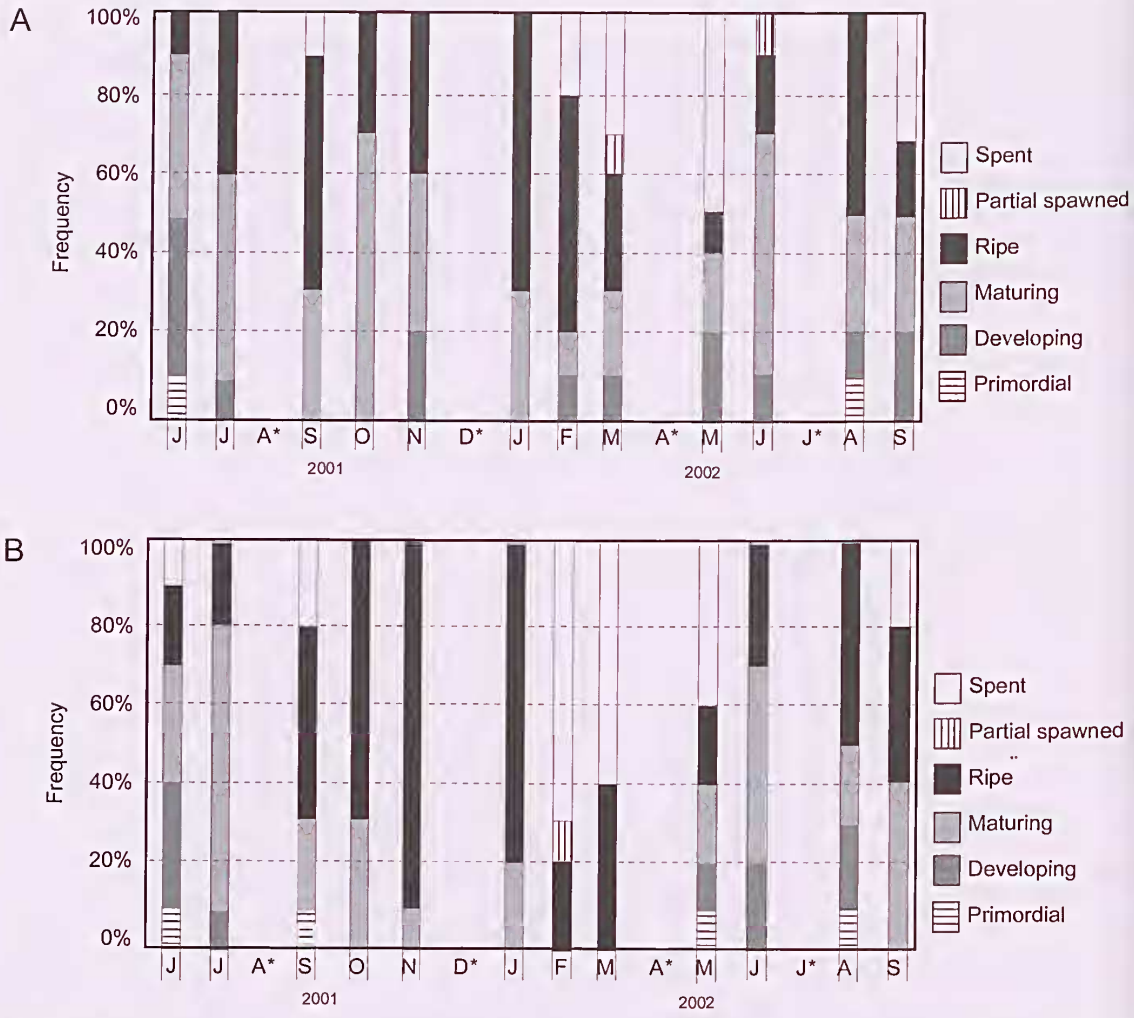

Fig. 7. Changes in histological rank for reproductive condition of **A**, male and **B**, female *Polymesoda erosa* from Maningrida between June 2001 and September 2002. * = no sampling during these months.

GSI values showed that females had larger gonads than males. This shows that the pattern of material accumulation during development of the gonads is different between males and females (Grant and Tyler 1983). Nevertheless, the present study showed there was a synchronous pattern of gonad development and spawning between the sexes.

Reproductive cycle. In general, the *Polymesoda erosa* population from Maningrida possessed mature individuals year round, as confirmed by the GSI, GI and histological data. However, the population showed some seasonality in spawning intensities. Continuous breeding with different spawning intensities is typical of tropical bivalves (Urban 2001). The *P. erosa* population at Maningrida had two major spawning periods (i.e., a short season in September and an extended season occurring between February and May). This gametogenic pattern is different to that of the *P. erosa* population in Hong Kong, where the local seasonal cycle creates a single extended breeding period over summer (Morton 1985).

Contrasting the two populations, there are clear differences in reproductive timing. In Hong Kong, *Polymesoda erosa* commences active gametogenesis between April and May with maturation during June and August. Spawning occurs at the end of summer and from September until the following February most individuals were still spent. Apparently this long recovery was affected by cold, winter water temperatures (Morton 1985). Conversely, at Maningrida, active gametogenesis starts in June, and by August most individuals have reached maturity. Rapid gametogenesis at Maningrida was proven by low percentages of early stages (primordial and developing) in the population throughout the year

(Cárdenas and Aranda 2000). At Maningrida, although a small proportion of the population spawns in September, most ripe individuals retain their gametes and remain at a mature stage for a long period until January. This condition is an indication of ripe gamete accumulation (Cárdenas and Aranda 2000). The period of 'ripeness' at Maningrida was extended by a second spawning season from February to May. In males, gonadal maturation takes place gradually to reach a maximum at the end of the season, whereas in females intense spawning occurs at the beginning of the season followed by spawning at reduced levels at the end.

The resting period in *Polymesoda erosa* from Maningrida was short, if not absent. An absence of a resting period is common in tropical bivalves where gonads recover soon after spawning is complete (Pouvreau *et al.* 2000; Laureta and Marasigan 2000; Urban 2001). A rapid recovery rate and no observable resting period in a population could only happen when the production of a new cohort of germinal cells takes place continuously (González *et al.* 2002). In the present study, even mature animals contained germinal cells at various early developmental stages. Also, during resorption of unreleased gametes, the gonad continues to produce new germinal cells as can be seen from the presence of oogonia and lytic ova in the same gonad. These findings could explain the fast recovery rate of the *P. erosa* gonad. The ability to recover enables individuals to have multiple spawnings throughout the year as long as specific cues are available (Marsden 1999).

Rapid redevelopment after spawning also happens when animals show partial spawning (Joll and Caputi 1995), or if spawning is incomplete (Rodríguez-Moscoso and Arnaiz 1998; Pouvreau *et al* 2000). Partially spawned specimens were recorded in *Polymesoda erosa* from Maningrida and Morton (1985) reported that for Hong Kong, even in ripe individuals, mature eggs never packed the follicles, suggesting a progressive release over a long period. This condition was also observed during this study. Such partial and incomplete spawning might contribute to the fast recovery of *P. erosa*. Newell *et al.* (1982) noted that 'dribble spawning' reduces the loss of potential recruits over the course of a year so that a catastrophic event kills few larvae.

At Maningrida, *Polymesoda erosa* shows asynchronous gamete development. The presence of two or more stages confirms this asynchrony (Fournier 1992; Tirado and Salas 1998). However, because ripe individuals do not release their gametes, those individuals which develop later reach the same stage as those which mature earlier. Consequently, some months (October to January) are dominated by ripe individuals. Such a situation reinforces synchrony, at least at maturation, increasing the chances of successful fertilization.

There was no evidence to link the spawning events of the Maningrida *Polymesoda erosa* population with changes in temperature, as suggested in subtropical Hong Kong (Morton 1985), or salinity. However, at Maningrida, seasonal temperature does not fluctuate as much as in Hong Kong, where temperatures rise above 35°C in summer but fall to near freezing in winter, and the fact that gametogenesis takes place rapidly in any month of the year suggests that temperature does not play a major role in directing gametogenesis in the tropics. Salinity can also regulate gametogenesis in marine bivalves (Giese 1959; Urban 2001), although how it affects gonadal maturation is unclear (Fournier 1992). In the present study, salinity measurements recorded a range of 5 to 40‰ among samples inside the mantle cavity, suggesting that *P. erosa* at Maningrida was exposed to considerable fluctuations in salinity. However, gametogenesis was not affected by rises or falls in salinity, as shown by the presence of various gamete developmental stages year round.

The ability to retain mature gametes without resorption for long periods of time (up to five months) in *Polymesoda erosa* is unusual but, possibly, happens in other tropical bivalves, e.g. the pearl oyster *Pinctada margaritifera* (Linnaeus) from tropical regions (Pouvreau *et al.* 2000). In most bivalves, ripe gametes that are not released soon after maturation are reabsorbed. In the scallop, *Argopecten purpuratus* (Lamarck), mature oocytes undergo atresia (lysis) and are later reabsorbed when retained too long (Avendaño and Le Pennec 1997). Low temperature and a lack of food are factors acting, independently or together, to cause atresia (Avendaño and Le Pennec 1997).

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